AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 105:395–403 (1998)

Technical Note: Chromosomal and mtDNA Analysis of Oliver

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KEY WORDS C-banding; chimpanzees; G-banding; karyotypes; phylogeography

ABSTRACT Oliver is an African ape whose species identity has been debated in the popular media and by various scientists since the early 1970s. Although decisive morphological data has never been adduced on Oliver, many reports indicated that Oliver was morphologically unusual for a chimpanzee, particularly in his habitual bipedal posture. In addition, his diploid chromosome number was reported to be inconsistent with either human or chimpanzee, but instead intermediate between those species. We performed standard chromosomal studies which demonstrated that Oliver had the diploid number expected for a chimpanzee (2N = 48) and that the banding patterns of his chromosomes were typical for a chimpanzee and different from both humans and bonobos. We also sequenced a 312 bp region of his mitochondrial DNA D-loop region. Results indicated a high sequence homology to the Central African variety of chimpanzee, *Pan troglodytes troglodytes*. The highest percent homology was observed with a previously characterized specimen from Gabon, strongly suggesting that Oliver originated from this region. Am J Phys Anthropol 105:395–403, 1998.

Oliver recently attracted the attention of the scientific community (Science, 1996; Laboratory Primate Newsletter, 1996) after he was acquired in 1996 by Primarily Primates, a private sanctuary for animals rejected by zoos, retired from research, rescued from the illegal pet trade, or confiscated from poachers. Believed to have been imported from the Congo River area of Central Africa in the 1960s, many questions of species identity have surrounded Oliver. Previous observers have suggested that a variety of unusual morphological or behavioral traits were inconsistent with Oliver's identity as a common chimpanzee (*Pan troglodytes*). Reportedly, his limbs were too long, his ears misplaced or irregularly shaped, and his head too small, bald, or dome-shaped for a chimpanzee. His locked-knee, bipedal gait and persistent rumors that he had a diploid (2N) number of 47 chromosomes, intermediate between humans (2N = 46) and chimpanzees (2N = 48), spurred popular speculation that Oliver was the "missing link" or a human-ape hybrid.

A cursory examination of Oliver's background revealed no evidence of any serious scientific study. Morphological measurements collected on Oliver by three previous owners or handlers consisted primarily of limb dimensions with a high degree of between-observer variability. Although many of these and other morphological features

Contract grant sponsor: NIH; contract grant number RR08083.

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Received 10 September 1997; accepted 30 October 1997.

have been compared among geographical varieties of chimpanzees (Groves, 1986), they typically lack a reference population for comparison and are too variable to be diagnostic (Albrecht and Miller, 1993). Furthermore, since Oliver was still alive and had only four molars, the more diagnostic dentometric and craniometric data could not be collected (Eckhardt, 1992; Groves et al., 1992). W.C. Osman Hill, the primate taxonomist, stated: "Chimpanzees. . .present a bewildering variety of individual variations. . . . [including] density and color of pelage, the presence or absence of bald areas, the pattern of. . .pigmentation, size of ears as well as cranial morphology" (Hill, 1969, p. 31). This list of normal physical variations includes most of the characteristics measured by Oliver's previous owners or emphasized in rumors, all of which are of questionable reliability in chimpanzee systematics (Hill, 1969).

Dr. Mitsuo Iwamoto, of the Primate Research Institute in Kyoto, Japan, appeared on a Nippon Television Network program, videotaped on 19 July 1976 and broadcast on 22 July 1976, which intended to scientifically determine "whether. . .Oliver can be the missing link." According to an English transcription of the broadcast, Dr. Iwamoto inspected a set of X-rays (reputedly taken at the Nippon Television Medical Center) and pointed out that Oliver's lumbar pelvis and jaws were like a chimpanzee's and unlike a human's, and that a minor abnormality in the placement of the maxillary bone could be attributed to Oliver's lack of teeth, which were apparently pulled at an early age. As reported in *Science*, the naturalist Dr. George B. Schaller examined Oliver in February, 1976 (Science, 1996). Dr. Schaller clearly dismissed the taxonomic significance of Oliver's bipedalism by stating "I believe that he [Oliver] is a chimpanzee but in his posture a highly unusual one" (Schaller, 1976, and personal communication). The well-known primatologist Dr. Clifford C. Jolly also examined Oliver in January 1976 and concluded that Oliver was a chimpanzee, but that the peculiar appearance of his lower face (including resorption of the alveolar bone, shortened maxilla and premaxilla, and underdeveloped temporal musculature) and his apparently small head size were due to his edentulous condition, while his bipedalism was due to conditioning (Jolly, 1976).

Despite many rumors, previous chromosomal evidence on Oliver was difficult to locate and evaluate. Karyotypes were thought to have been performed by Japanese scientists (Science, 1996), yet Dr. Iwamoto stated that "we took his [Oliver's] blood too late" to culture cells for a karyotype (Anonymous, 1976). Instead, he was shown a karyotype attributed to unidentified "American scholars" which depicted 47 chromosomes accompanied by a question mark. The persistent ambiguity and uncertainty concerning genetic studies supposedly performed in the past led us to conduct our own genetic analyses. We present here a genetic assessment which definitively resolves Oliver's species identity. We used standard cytogenetic techniques to determine whether Oliver could be correctly designated as a chimpanzee or whether he represented a hybrid cross and we studied Oliver's mitochondrial DNA sequence to ascertain his phylogeographical origins.

METHODS

Cytogenetic methods

A peripheral blood sample was collected from Oliver during a routine medical examination and shipped to our (CMM) cytogenetics laboratory. The blood was cultured in RPMI 1640 with 15% fetal bovine serum and Concanavalin A (30 µg/ml). It was incubated for 72 hr at 37°C, arrested with Colcemid, treated with hypotonic KCl solution and fixed with 3:1 methanol:acetic acid. Air-dried slides were prepared and heated for 45 min at 90°C in a dry oven. Standard GTG- and C-banding was performed. Ten cells were analyzed with G-banding. All metaphases had a count of 48 chromosomes. From these cells, four karyotypes were prepared and arranged according to the ISCN (1985) recommendations for the great apes. C-banding patterns were examined in 18 cells for centromeric, interstitial, and terminal heterochromatin.

DNA methods

The remaining blood sample was delivered to our (JJE) molecular genetics labora-

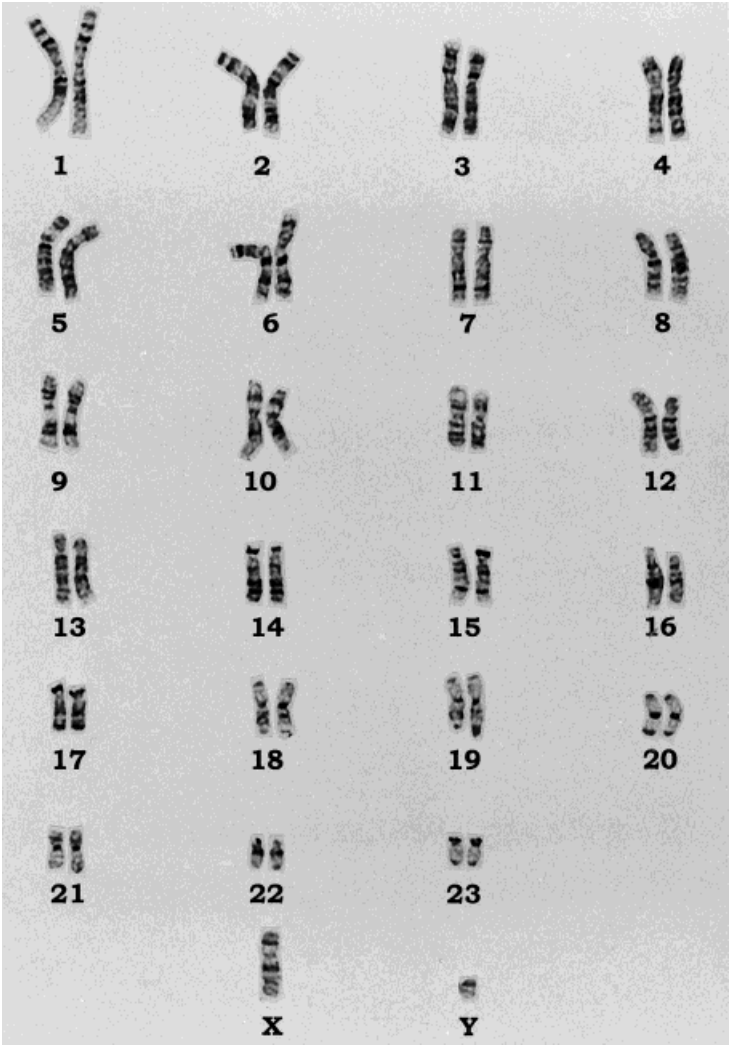

Fig. 1. G-banded karyotype of Oliver. Karyotype is arranged according to ISCN (1985) recommendations for the great apes. Note the presence of two copies of chromosomes 12 and 13 (homologues of *Homo sapiens* [HSA 2]), with a chromosomal count of 48.

tory for PCR and DNA sequence analysis. DNA was extracted by a salting-out procedure (Miller et al., 1988). Preliminary PCR tests indicated that little nuclear DNA survived the week-long processing. However, the sample was rich in mitochondrial DNA (mtDNA). PCR primers (For: 5′-CAACCGCTATGTATTTCGTA-3′ = bases 55–74; Rev: 5′-GCGGGATATTGATTTCAC-3′ = bases 388–405) were used to amplify a 313 bp segment of the chimpanzee mtDNA control region (Arnason et al., 1996) containing numerous polymorphic nucleotide sites (Kocher and Wilson, 1991) which are phylogeographically informative (Morin et al., 1994). PCRs were performed with 1.0 U of *pfu* DNA polymerase (Stratagene, La Jolla, CA), a high-fidelity DNA polymerase with both 5′→3′ and 3′→5′ proofreading activity (Cline et al., 1996). PCR cocktails consisted of 100 ng of each primer, 200 mM dNTPs, 1.5 mM $MgCl_2$, 1X manufacturer-supplied PCR buffer, and 50 ng mtDNA template in a total reaction volume of 50 µl and amplified with

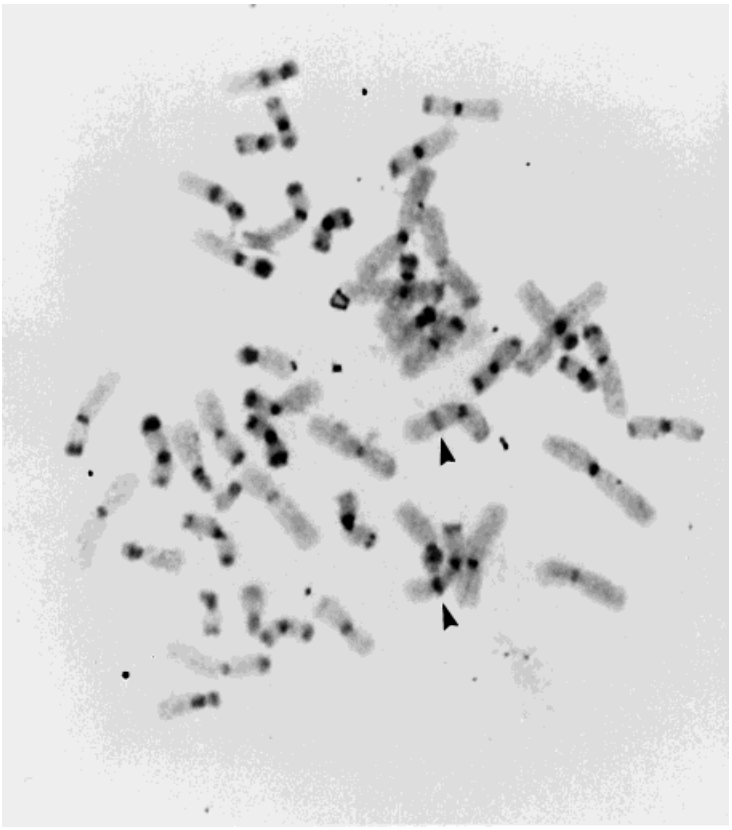

Fig. 2. C-banded metaphase of Oliver. Note the interstitial heterochromatin in *Pan troglodytes/Pan paniscus* (PTR/PPA) chromosome 6 at arrows.

a Perkin/Elmer GeneAmp 9600 thermal cycler. Amplification product was separated in a 1% LMP agarose gel, column purified (Promega, Wizard PCR Preps, Madison, WI), then cycle-sequenced on a MJ-PTC100-96V thermal cycler using ^{33}P-labeled ddNTPs, according to manufacturer's (Amersham, ThermoSequenase, Arlington Heights, IL) recommendations. PCR product was diluted 1:1 in a formamide loading dye (Sambrook et al., 1989), denatured at 94°C for 5 min, then loaded into a pre-warmed 6% denaturing polyacrylamide gel and electrophoresed at 55 W for a long (2.5 hr) then a short (1.5 hr) run. The gel was vacuum dried for 60 min onto 3 mm filter paper, exposed to Kodak XAR-5 X-ray film for 3 days at room temperature, then developed. DNA sequences were read manually and confirmed with forward and reverse sequencing reactions.

TABLE 1. Differences in G- and C-banding patterns of four chromosomes distinguishing Pan troglodytes *and* Pan paniscus *compared with* Homo sapiens[1]

Homo sapiens (HSA) Human	*Pan troglodytes* (PTR) Chimpanzee	*Pan paniscus* (PPA) Bonobo
2	fusion	fusion, **pericentric inversion on 13**[2]
7	interstitial heterochromatin in 6q terminal heterochromatin	interstitial heterochromatin in 6q terminal heterochromatin **paracentric inversion on 6q**
13	1 additional G-band	**2 additional G-bands**
14	—[3]	**1 additional G-band**

[1] After Stanyon et al. (1986).
[2] Bold indicates a difference between PTR and PPA.
[3] No chromosomal differences between HSA and PTR.

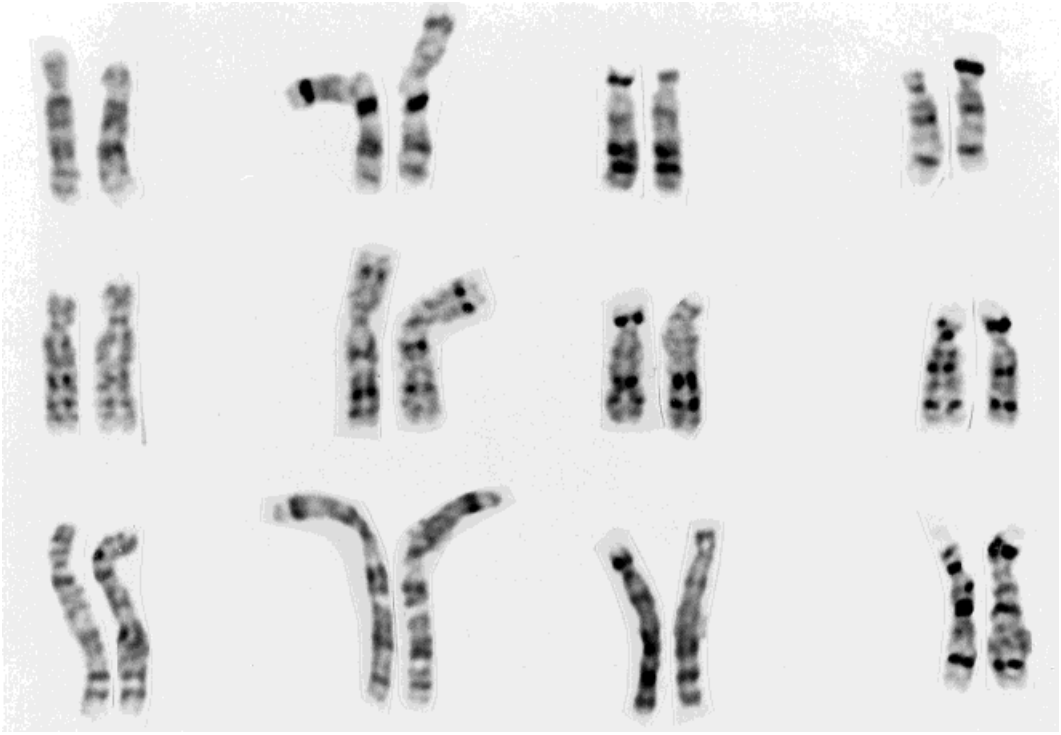

Fig. 3. Four pairs of Oliver's chromosomes (PTR/PPA 13, 6, 14, and 15) taken from three separate cells. Note normal polymorphisms in centromeric and terminal heterochromatin.

mtDNA sequence comparisons

Homology searches were conducted against catalogued GenBank DNA sequences using the BLAST routine (Altschul et al., 1990), available at the National Center for Biotechnology Information (NCBI) web site (http://www.ncbi.nlm.nih.gov/cgi-bin/BLAST/-blast). For *Pan troglodytes troglodytes*, *P. t. schweinfurthii*, *P. paniscus*, and *Homo sapiens*, percent homology and the probability of the observed match were estimated by BLAST. Since *P. t. verus* sequences were too dissimilar to be evaluated by BLAST, percent homology was calculated by hand and no probability of the observed match was made.

RESULTS

Cytogenetic results

The G- and C-banding patterns of Oliver's chromosomes were compared to those of the human, *H. sapiens* (HSA), the chimpanzee, *P. troglodytes* (PTR) (ISCN, 1985; Yunis and Prakash, 1982), and the pygmy chimpanzee or bonobo, *P. paniscus* (PPA) (Stanyon et al., 1986). Both the G- and C-banding patterns were consistent only with those of PTR (Figs. 1, 2). The chromosomal count of 48 with the presence of two copies each of chromosomes PTR/PPA 12 and 13 (homologues of HSA 2p and 2q, respectively) clearly distinguished Oliver's cells from those of HSA. Four chromosomes have been reported to have consistent differences between PTR and PPA: PTR/PPA 6, 13, 14, and 15, which are homologous to HSA 7, 2q, 13, and 14, respectively (Table 1). For all four, both of Oliver's homologues exhibited the banding pattern of PTR (Fig. 3).

mtDNA sequencing results

The 50 best-matching DNA sequences selected by the BLAST routine were all from chimpanzees, with at least 88% homology to

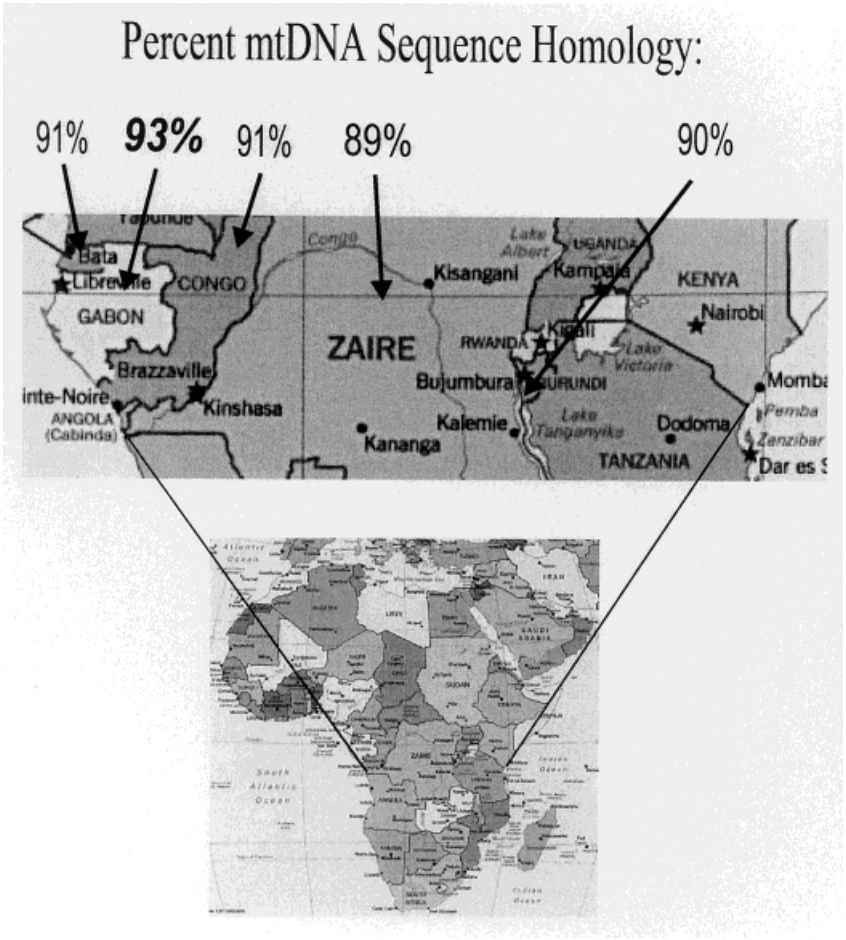

Fig. 4. Median percent mtDNA sequence homology declines in both directions from Gabon. *Pan t. troglodytes* is found in Equatorial Guinea, Gabon, and the Congo. *Pan t. schweinfurthi* is found in Zaire, Burundi, and Tanzania, including Gombe. *P. t. verus* (not represented here) is found from Senegal to Central Nigeria.

Oliver's mtDNA sequence. Both the highest sequence homology (95%) and the lowest probability of observing the given match by chance (2.5×10^{-114}) were with "Tina," a zoo chimpanzee attributed to the Central African *P. t. troglodytes* variety (Aranson et al., 1996) on the basis of mtDNA sequence homology to chimpanzees of known geographical origins (Morin et al., 1994). The best fitting mtDNA sequence with a known geographical origin was "Mopia" (Genbank Accession #35401), a *P.t. troglodytes* from Haut-Ogooue, Gabon, with 94% sequence homology and a probability of 2.9×10^{107} of occurring by chance. The identification of Gabon as Oliver's probable country of origin was corroborated by examination of all 43 *P. t. troglodytes* mtDNA sequences selected by BLAST which had known geographical origins. Moving along the equator through Central Africa, the median percent sequence homology decreased the further away one moved, either east or west, from Gabon (see Fig. 4).

Due to reduced sequence homology, the BLAST alignments did not include the West African chimpanzee, *P. t. verus*. To compare Oliver to *P. t. verus*, *P. paniscus* and

Olv75[1,2]: cattactgcc agccaccatg aatattgtac agtactataa tcactcaact acctataaca cattaaaccc -acc-cc-ac
Ptt 75[3]: cattactgcc agccaccatg aatattgtac agtactataa tcactcaact acctataaca cattaaaccc -acc-cc-at
Ptv 75[4]: cattactgcc agccaccatg aatatcgtac agtaccata- tcacccaact acctatagta cataaaatcc -act-cccac
*Pts*75[5]: cattactgcc agccaccatg aatattgtac agtactataa tcactcaact acctataaca cattaaaccc -acc-ccata
Ppa 75[6]: cattactgcc agccaccatg aatattacat agtactataa tcatttaacc acctataaca cataaaaacc tacatcc-ac
*Hsa*75[7]: cattactgcc agccaccatg aatattgtac ggtaccataa atacttgact acctgtagta cataaaaacc -aac-cc-ac

Olv155: attacaacgt ccccccc-at gcttacaagc acgtacaaca atcaaccctc aactgtcaca cataaaacgc aactccaaag
*Ptt*155: attacaacat --------at gcttacaagc acgtacaaca atcaaccctc aactgtcaca cataagacgc aactccaaag
*Ptv*155: atcaaaacct tcactcc-at gcttacaagc acgcacaaca atcaactc-c aactgtcgaa cataaaacac aattccaacg
*Pts*155: -ttacaacat --------at gcttacaagc acgtacaaca atcaaccctc aactgtcaca cataagacgc aactccaaag
*Ppa*155: attaaaaccc ccccccc-at gcatataagc acgaacaata atcgacctcc aactgtcgaa cataaacacc ccc-ccaaag
*Hsa*155: atcaaaatcc tacccccc-at gcttacaagc aagtacagca atcaaccttc aactgtcaca catcaactgc aactccaaag

Olv235: acactcctcc cccaccccga taccaacaaa cctacactcc c-ttaacagt acatagcaca tacaaccgca caccag-aca
*Ptt*235: acactcctcc cccaccccga taccaacaaa cctacactcc c-ttaacagt acatagcaca tacaaccgca caccag-aca
*Ptv*235: acacccctcc cccaccccga taccaacaga cctat-ctcc ccttgacaga acatggtaca tacaaccata cacc-gtaca
*Pts*235: acactcctcc cccaccccga taccaacaaa cctacactcc c-ttaacagt acatagcaca tacaaccgca caccag-aca
*Ppa*235: acactccccc cccaccccga taccaacaaa cctgacagtc c-ttaacagt acatagcaca tacaattata tacc-gtaca
*Hsa*235: ccacccctca cccactagga taccaacaaa cctaccacc c-ttaacagt acatagcaca taaagtcatt tacc-gtaca

Olv315: tagcacatta cagtcaaatc cattctcgcc cccacggatg ccccccctca gataggagtc ccttgctcac catcctcc
*Ptt*315: tggcacatta tagtcaaatc cattctcgtc cccacggatg -------tca gataggggtc ccttgctcac catcctcc
*Ptv*315: tagcacatta cagtcaaacc cctcctcgcc cccacggatg ctcccccctca gataggaatc ccttggtcac catcctcc
*Pts*315: tggcacatta tagtcaaa
*Ppa*315: tagcacatta cagtcaaatc catcctcgcc cccacggatg ccccccctca gataggaatc ccttggccac catcctcc
*Hsa*315: tagcacatta cagtcaaatc ccttctcgtc cccatggatg acccccctca gataggggtc ccttgaccac catcctcc

Fig. 5. Comparison of Oliver's mtDNA sequence to chimpanzee, human, and bonobo.

TABLE 2. Summary of comparative mtDNA sequence homology alignments

Species	Geographical origins of specimen	ID	% Homology	P^1	GenBank accession number	References
P.t. troglodytes	Central Africa	Tina	95%	2.5×10^{-114}	X93336	Arnason et al., 1996
	Gabon	Mopia	94%	2.9×10^{-107}	L35401	Morin et al., 1994
P.t. schweinfurthii	East Africa	Gigi	91%	1.3×10^{-95}	L35391	Morin et al., 1994
P.t. verus	West Africa	C3	86%	—	—	Arnason et al., 1996; Kocher and Wilson, 1991
Homo sapiens	unknown	—	84%	6.9×10^{-79}	D38112	Horai et al., 1995
Pan paniscus	Zaire	—	83%	2.0×10^{-73}	D38116	Foran et al., 1988; Horai et al., 1995

[1] The probability of obtaining the observed degree of sequence similarity by chance. A smaller probability indicates a closer phylogenetic relationship.

H. sapiens, Genbank sequences were aligned manually (see Fig. 5). For these particular specimens, the maximum homology of 95% was observed in Tina, a Central African *P. t. troglodytes*, with slightly less homology in an East African *P. t. schweinfurthii* (91%), still less in a West African *P. t. verus* (86%), then declined to 84% for *H. sapiens* and 83% for *P. paniscus*. These comparative data are summarized in Table 2.

DISCUSSION AND CONCLUSIONS

Our original inspection of Oliver's background file revealed a photograph of Oliver's karyotype with a "?" printed over the space left empty by a missing chromosome 15 homologue. Following completion of our own studies, further karyotypes were found in Oliver's background file, together with associated documentation signed by Momoki Hirai, a cytogeneticist at the Genetics Division of the National Institute of Radiological Sciences in Chiba-shi, Japan. That report indicated that 38 of 40 conventionally stained (unbanded) metaphase spreads had the 48 chromosomes expected for a chimpanzee, while the remaining two spreads had only 47 chromosomes. One of Hirai's attached karyotypes indicated a missing chromosome 10 homologue. "The cells with 47 chromosomes were presumable the product of artefact, since a number of cells were broken during the process of preparation" (Hirai, n.d., p. 2). Hirai also commented on the C-banding patterns he examined, noting that Oliver's C-banding pattern was different from that of humans. In particular, Oliver's Y chromosome lacked the distal heterochromatic C-band at Yq12, which is commonly found in humans but not in chimpanzees (ICSN, 1985). Hirai correctly concluded that Oliver was a chromosomally typical chimpanzee, with the obvious and expected chromosomal differences compared to humans, while the anomalous chromosome spreads occurred at a statistically acceptable error rate of 5% (2/40). The karyotype with a "47?" printed in the empty space of a missing chromosome 15 homologue, which we found in Oliver's background file, remains of unknown origin. However, this photograph found its way into the media, for example, in the Nippon Television Network broadcast, and was widely cited as evidence that Oliver was chromosomally abnormal for a chimpanzee.

Our genetic studies confirmed and extended these earlier, unpublished results. Our cytogenetic analysis of G- and C-banding patterns excluded the possibility that Oliver was either a chimpanzee/bonobo (Vervaecke and Van Elsacker, 1992) or a human/chimpanzee hybrid. Instead, Oliver has a karyotype consistent with that of the common chimpanzee, *P. troglodytes*. The mtDNA evidence supported these conclusions: Oliver had only weak mtDNA sequence homology (83–84%) to both humans and bonobos. Furthermore, Oliver's mtDNA sequence was consistent with previously documented sequence variants of chimpanzees and exhibited a reduced homology to East and West African varieties of chimpanzee (89–90%), but a much stronger (94%) fit to a previously characterized Central African *P. t. troglodytes* variant from Gabon. Thus, the genetic evidence presented here is completely consistent with Oliver being a *P. t. troglodytes* chimpanzee from Central Africa, most probably Gabon.

ACKNOWLEDGMENTS

We thank Kathy Brasky, D.V.M., Anthony Comuzzie, Ph.D., Daniel Gonzalez, Xavier Reveles, and William H. Stone, Ph.D., for their advice and assistance.

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